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# The Relationships of *Solanum cochoae* (Solanaceae), a New Species from Peru

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The genus *Solanum*, with nearly 3,500 epithets, is second only to *Senecio* in size, and its species are notoriously variable (Correll, 1962). Growing appreciation for intraspecific variation has helped make recognition of species boundaries more realistic to the point that only about one-half of the species that have been described are now accepted (D'Arcy, 1979). This daunting diversity and variability gives one pause in describing a new species. Thus, we have grown and studied the subject of this paper for some time; we are now convinced it deserves recognition as a distinct species. The diagnosis and description of this new species follows the discussion of its systematic uniqueness and relationship.

## MORPHOLOGICAL FEATURES

Like many species of *Solanum*, or at least species in subg. *Potatoe*, *S. cochoae* is morphologically distinct, but this distinction is based on a combination of characters, no one of which is unique to *S. cochoae*. This means that taxa may be characterized by a combination of nonunique characters (homoplasious features).

The species from *Solanum* sect. *Basarthrum* (Bitter) Bitter that are morphologically similar to *S. cochoae* are given in Table 1, with the characters that distinguish each from *S. cochoae* marked with an asterisk. As is clear from these data, *S. cochoae* can be readily distinguished from its most similar relatives. It is a member of series *Caripensia* Bitter & Sodiro and is most like the following species: *S. caripense* Humb. & Bonpl. ex Dunal, *S. tabanoense* Correll, *S. basendopogon* Bitter, *S. trachycarpum* Bitter & Sodiro, *S. filiforme* Ruiz Lopez & Pavón, *S. fraxinifolium* Dunal in DC, and *S. heiseri* G. J. Anderson. The last three are sibling species of *S. caripense* and are represented in Table 1 by *S. caripense*. Five other species are included in Table 1 because they are morphologically similar to *S. cochoae*. *Solanum muricatum* Aiton, *S. suaveolens* Kunth & Boché, and *S. canense* Rydb. are also from series *Caripensia*. The other two species, *S. taeniotrichum* Correll and *S. sanctae-marthae* Bit-

ter, are superficially confusable with *S. cochoae*, but are probably not closely related (Anderson et al., 1987). *Solanum cochoae* is characterized within series *Caripensia* as the only species with compound leaves and with a branched inflorescence bearing an average of more than 20 flowers (Fig. 1). Within section *Basarthrum* as presently circumscribed, it is the only species with these characters (Table 1) and with two-celled "bayonet" hairs (Seithe & Anderson, 1982) (see Fig. 1). In addition to these quantitative differences, *S. cochoae* is distinguished from the *S. caripense* complex by such qualitative differences as the generally pale yellow/white anthers (vs. orange-yellow) and the more compact, headlike inflorescence (vs. elongate raceme).

## CROSSING STUDIES

Intraspecific crosses (see Table 2) confirm that this species is, like the vast majority of others in section *Basarthrum* (Anderson, 1979), self-incompatible: none of more than 150 intraplant ("self") crosses were successful. On the other hand, almost one-half of the interplant crosses were successful, and the resulting seeds germinated readily to produce highly fertile plants (pollen fertility  $\bar{x}$  value = 98%, "fertility" assayed by staining with aniline blue in lactophenol). The degree by which the style exceeds the staminal column ( $\bar{x}$  = 1.7 mm, Table 1) is very close to the average ( $\bar{x}$  = 1.9) for the self-incompatible (outcrossing) species previously recognized for section *Basarthrum* (Anderson, 1979) and thus adds support for this generalization in *Solanum*.

More than 900 crosses were attempted between *S. cochoae* and its seven morphologically most similar, related wild species (Table 2). A good percentage of these resulted in fruit, but virtually all produced fruits with very few seeds, and none of the seeds germinated. Thus, no crosses with any related wild species were successful.

Crosses were also attempted with the cultivated domesticate, *S. muricatum* ("pepino dulce"). About 10% of these crosses were successful regardless of

TABLE 1. Distribution and characters of morphologically similar species. Characters distinguishing each species from *Solanum cochoae* are marked with an asterisk (\*). All measurements and means are in millimeters. Species codes are as follows: COCH = *Solanum cochoae*; CARI = *S. caripense*; TABA = *S. tabanoense*; BASE = *S. basendopogon*; TRAC = *S. trachycarpum*; MURI = *S. muricatum*; SUAV = *S. suaveolens*; CANE = *S. canense*; TAEN = *S. taeniotrichum*; and SANC = *S. sanctae-marthae*.

		Species codes									
		COCH	CARI	TABA	BASE	TRAC	MURI	SUAV	CANE	TAEN	SANC
Distribution	Peru		Central & South America	South America	Peru	Ecuador	South America	South America (Central America)	Central America (South America)	Costa Rica	Colombia
Fruit color	green	green, purple stripes	green, purple stripes	green, purple stripes	green	green	green, cream,* purple*	green	green	red*	green
Fruit surface	smooth	smooth	smooth	smooth	warty*	verrucose*	smooth	smooth	smooth	smooth	smooth
Habit	viny bush	viny bush	viny bush	viny bush	small shrub*	small shrub*	small shrub*	lax herb*	lax herb*	viny bush	viny bush
Hair types	bayonet	bayonet	bayonet	bayonet	bayonet	bayonet	bayonet	bayonet	bayonet	finger*	finger*
Inflorescence axes	2	1*	1*	1*	3.2*	1*	1-3	1.1*	2	4*	2
Flowers/inflor- cense	26.7	10.9*	10.5*	10.5*	19*	2.1*	9.7*	9.5*	17.0*	42*	19*
Corolla lobe length	8.4	8.3	9.6	9.6	7.6	7.4	10.7	6.1	6.2	15.5*	10.8
Corolla lobe/sinus	1.6	1.7	4.0*	4.0*	1.5	1.7	1.9	1.4	2.5*	1.4	1.6
Anther length	3.5	3.8	5.4	5.4	4.0	2.6	3.7	3.0	2.9	4.3	5.6*
Style length	5.7	5.9	7.1	7.1	6.9	4.1	6.3	3.2*	3.8	7.0	7.0
Style past anthers	1.7	1.9	2.2	2.2	2.1	0.7*	2.6	0.1*	0.7*	—	—

TABLE 1. Continued.

	Species codes										
	COCH	CARI	TABA	BASE	TRAC	MURI	SUAV	CANE	TAEN	SANC	
Leaflets	4.3	4.8	1.2*	1*	1*	1-7	9.6*	10.9*	5	3-7	
Terminal leaflet length	44.6	33.5	52.3	34.8	33.1	72.5*	47.3	48.8	66.7*	76*	
Terminal leaflet length/width index	1.66	1.74	2.9*	1.85	1.89	0.83*	3.9*	3.2*	2.8*	2.4	



Figure 1. *Solanum cochoae*. —A. Branch of plant showing compound leaves and branched inflorescence. —B. Representative two-celled bayonet hairs. —C. Flower with moderately reflexed corolla and style exceeding staminal column. —D. Androecium and gynoecium with short hairs on adaxial face of filaments and over lower 75% of style. Scale bars = 1 mm.

the direction of the cross (Table 2). Few seeds were set, few of these germinated, but the resulting  $F_1$  hybrids had surprisingly high pollen fertility ( $\bar{x} = 86\%$ ,  $n = 18$ ).

*Solanum cochoae* appears to be isolated by breeding barriers from the wild species that are morphologically and/or geographically closely allied to it. The relative crossing success with *S. muricatum* is of interest, because *S. cochoae* now must be considered along with *S. basendopogon*, *S. caripense*, and *S. tabanoense* (Anderson et al., 1987; Heiser, 1985) as one of the possible progenitors of this exclusively domesticated species.

#### CHROMOSOME MORPHOLOGY

Publication of detailed analyses of the karyotypes of species of section *Basarthrum* included this new species as "934" (Bernardello & Anderson, 1990). Karyotypically *S. cochoae* is, as might be predicted, most similar to the other wild species in series *Caripensia* and to *S. muricatum*. The karyotype for *S. cochoae* consists of the following chromosomes: five metacentrics, six sub-metacentrics, and one sub-terminal. Four other species have a subterminal chromosome: *S. muricatum*, *S. fraxinifolium*, *S. canense*, and *S. suaveolens*. The last three have

significantly smaller chromosomes overall than *S. cochoae*. The genome of *S. muricatum* is different from that of *S. cochoae* in a number of ways: two of the more significant are that *S. muricatum* bears a telocentric, and eight chromosomes have different arm ratios and are longer.

Overall genome homology of *S. cochoae* and *S. muricatum* is implied as well by the high fertility of  $F_1$  hybrids between them. The "cochoae" genome apparently even acts as a "fertility restorer":  $F_1$  hybrids have almost twice the pollen fertility ( $\bar{x}$  = 86%) of the "muricatum" parent ( $\bar{x}$  = 47%).

#### FLAVONOIDS

*Solanum cochoae*, as "934," was characterized by six of the 11 flavonols recognized for section *Basarthrum* (Anderson et al., 1987). There are no unique compounds delineating *S. cochoae*. The species with most similarity (based on a Manhattan Distance estimate) to *S. cochoae* are those from series *Caripensia* (*S. tabanoense* 17%, *S. filiforme* 33%, *S. trachycarpum* 44%, *S. muricatum* 50%, *S. basendopogon* 56%, *S. suaveolens* 57%, *S. caripense* 60%, *S. fraxinifolium* 62%, *S. heiseri* 62%, *S. canense* 67%). However, there are several other species in the section associated with *S. cochoae* at close to the 40% level, so these values do not constitute a strong argument for the exclusive membership of *S. cochoae* in series *Caripensia*, or alternatively, for using flavonoids as characters verifying the cohesiveness of this series.

#### DISCUSSION

The successful crosses with the pepino dulce (*S. muricatum*) are of special interest. *Solanum cochoae* now becomes one of only four species that has been crossed successfully with the pepino dulce (Anderson, 1979; Heiser, 1985). The relatively high fertility of the  $F_1$  hybrids between these two species may indicate a place for *S. cochoae* in the ancestry of the pepino dulce, an issue of interest not only in determination of the origin of this cultigen, but potentially for its improvement through breeding as well. The  $F_1$  hybrids are also of interest because they are self-compatible. The pepino dulce accessions used were all self-compatible, and the *S. cochoae* accession is self-incompatible. Thus, the self-compatibility of the  $F_1$ s seems to document the dominance of genes or alleles for this breeding system character state at least in this section of *Solanum*.

By virtue of the articulation of the pedicels at their base, lack of tubers (Correll, 1962), and two-celled bayonet hairs (Seithe & Anderson, 1982), *S.*

TABLE 2. Crossing studies among *Solanum cochoae* and its relatives. Codes are: F = very few hybrid seeds produced; H = high germination of hybrid seeds; L = low germination of hybrid seeds; N = no germination of hybrid seeds; Ph =  $F_1$  pollen fertility high. Fractions in parentheses give the number of crosses successful over the number attempted.

<i>Solanum cochoae</i>	Intraplant 0% (0/165)	Interplant 42% (53/126) H, Ph
	<i>S. cochoae</i> as:	
	Female parent	Male parent
<i>S. muricatum</i> (cultivated)	8% (8/96) F, L, Ph	12% (19/163) F, L, Ph
<i>S. basendopogon</i>	2% (2/124) F, N	0% (0/120)
<i>S. caripense</i>	2% (3/146) F, N	65% (43/66) F, N
<i>S. filiforme</i>	8% (1/12) F, N	—
<i>S. fraxinifolium</i>	0% (0/82)	39% (12/31) F, N
<i>S. heiseri</i>	0% (0/50)	0% (0/17)
<i>S. tabanoense</i>	0% (0/2)	0% (0/19)
<i>S. trachycarpum</i>	0% (0/14)	0% (0/22)

*cochoae* is best placed in *Solanum* sect. *Basarthrum*. Within the section, *S. cochoae* is very similar to the widespread and highly variable *S. caripense* and sibling species (see above). In spite of its overall similarity to members of the *S. caripense* complex, clearly *S. cochoae* constitutes a distinct species. Morphologically, cytologically, and chemically, it bears distinguishing features. These coupled with the virtual lack of production of viable hybrids in close to 1,000 crosses with its closest wild relatives argue strongly for its unitary evolutionary role.

#### Key to the species of *Solanum* section *Basarthrum* series *Caripensia*

- 1a. Leaves primarily simple.
  - 2a. Inflorescence branched . . . . . *S. basendopogon*
  - 2b. Inflorescence not branched.
    - 3a. Corolla rotate . . . . . *S. trachycarpum*
    - 3b. Corolla stellate . . . . . *S. tabanoense*
- 1b. Leaves primarily pinnately compound.
  - 4a. Inflorescence branched.
    - 5a. Viny bush, fruits smooth surfaced, flowers usually about 20–25 per inflorescence . . . . . *S. cochoae*
    - 5b. Upright subshrub, fruits verrucose or

- warty, flowers usually 20 or less per inflorescence . . . . . *S. basendopogon*  
 4b. Inflorescence simple . . . . .  
 . . . . . *S. caripense* complex (including *S. caripense*, *S. filiforme*, *S. fraxinifolium*, and *S. heiseri*)

***Solanum cochoae*** G. J. Anderson & Bernardello, sp. nov. TYPE: Peru. Amazonas: Prov. Chachapoyas, Dist. Maino, Convent, alt. 2,800 m, 31 Mar. 1979, C. Ochoa 13249 (holotype, US; isotypes, F not seen, GH not seen, WI not seen). Figure 1.

Plantae suffrutex; folia in foliola 3–5 divisa; indumentum duo cellulis pugioti pili; inflorescentia furcatus plerumque cum 20–30 floribus; pedicelli basaliter articulati.

Viny or trailing shrub, branches up to 1 m long, internodes 20–80 cm, with moderately dense, strigose vesture of two-celled bayonet hairs throughout and scattered short gland-tipped hairs, stem woody or thick-herbaceous, older branches occasionally rooting at the nodes; leaves with 3–5 leaflets, 80–100 mm long (holotype 149 mm), with petiole 18–30 mm long (holotype 49 mm); leaflets lanceolate to lanceolate-elliptic, base obtuse to truncate, apex acute to acuminate, with moderately dense, strigose vesture of two-celled bayonet hairs, glandular hairs sparse on both surfaces; terminal leaflet somewhat larger than the first pair of lateral leaflets, 36–55 mm long (holotype 68 mm), 19–31 mm wide; first pair of lateral leaflets 30–40 mm long (holotype 49 mm), 9–20 mm wide, short petiolulate; pseudostipules lacking; inflorescence a pseudoterminal and/or lateral raceme with 2 (rarely 3) axes and 15–61 flowers; pedicels 6–11 mm long, basally articulate, densely strigose vesture of two-celled bayonet hairs intermixed with short gland-tipped hairs; corolla white, rotate, moderately reflexed, lobes 5.5–9.5 mm long, sinuses 4–6 mm long, lobe/sinus ratio about 1.6, glabrous adaxially, sparsely strigose to hispid abaxially; calyx green, acute to acuminate, about ¼–⅓ the length of the corolla lobes, strigose vesture moderate to heavy; anthers pale yellow, apices rounded, 2.2–3.8 mm long, glabrous abaxially, a few scattered stiff hairs adaxially; filaments 1.5–2.7 mm long (holotype 0.7 mm), fused for less than ¼ of their length, scattered stiff hairs along their margin; style 3.9–6.5 mm long, sparingly strigose over lower ¾ of its length, hairs intermeshing with those of the anthers, stigma slightly capitate, exceeding staminal column by 1–2 mm; fruits globose to elliptic-ovoid, mature fruits yellow-orange with darker orange-brown arms from pedicel to style scar, 20–30 mm long and 13–18 mm wide, surface smooth; seeds 60–200 per fruit, lenticular, flattened

with narrow wing around margin of seed, 1.9–2.2 mm long by 1.4–2.0 mm wide, about 0.4–0.7 mm thick, brown, surface smooth to slightly rugose; pollen tricolporate, 15–18 µm diam., exine granular; mean pollen quantity 332,000 grains per flower; mean ovule quantity 146 per flower; mean pollen:ovule ratio 2315:1;  $n = 12$ . (See Table 1 for some average characters.)

*Phenology and distribution.* The only collection of this species to date, from near Chachapoyas, Peru, was in flower. Glasshouse-cultivated specimens flower year-round.

We have also studied an isotype from Carlos Ochoa's personal herbarium. Correspondence with the herbaria cited as housing the isotypes failed to yield the specimens. Thus, the bulk of the study was focused on a large number of plants grown from seed of the type collection. Specimens cultivated (GJA #934) in glasshouses at the University of Connecticut as part of this study have been deposited in CONN, CORD, MO, WI, and US.

This species is named in honor of Carlos Ochoa, who collected it and has made many important contributions to the systematics of *Solanum* through his fieldwork and writing.

In correspondence, Ochoa gave the following additional collection information “. . . near Maino, some 15 km (air distance) southeast of Chachapoyas, 2600–2800 m alt. . . . Plants of more than 1 m in height with long-conic berries, 2–3 cm long and 1.5–1.8 cm in the maximum transversal diam., yellow when ripe, edible according to local information. Vernacular name: *Pepinillo*.”

Ochoa also noted that the plant collected was growing in association with *Bidens andicola*, *Oyedaea buphthalmoides*, *Desmodium mollicolum*, *Cassia* sp., *Triunfetta calycina*, *Axonopus scoparius*, *Cyperus hermaphroditus*, *Solanum furcatum*, *Crotalaria nutans*, and *Lupinus allworthianus*.

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